Douglas-fir Productivity: A Conceptual Model of Its Regulation by Water and Nutrient Availability

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Productivity of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) forests is regulated by water and nutrient availability and by interactions between water and nutrient availability. The biological and physical basis for development of a conceptual model of forest productivity and is further developed in this paper. Potential site productivity is described as a function of leaf area. Leaf area is regulated by water availability; maximum site productivity is then set by the amount of water available to support transpiring leaf area. The proportion of this potential actually achieved appears to be a function of mineral nutrient availability. Mineral nutrition regulates stand leaf area, photosynthetic efficiency of foliage, autotrophic respiration and allocation of production to foliage, fine roots and mycorrhizae, and woody tissues.

INTRODUCTION

The purpose of this paper is to show how various factors of the physical and biological forest environment interact to regulate productivity of Douglas-fir ecosystems. The research underlying the results reported here was conducted in various coniferous forests of the western United States, excluding Alaska. A large proportion of these forests are dominated by Douglas-fir.

Earlier studies of productivity of Douglas-fir forests have concentrated on examining relations between site index, age, and yield, or on developing empirical associations between soil characteristics and site index. As a result, considerable effort in research has gone into developing and improving site index functions (King 1966), yield equations (McArdle *et al.* 1961), and in examining relations between soil characteristics and site index (Steinbrenner 1979a, 1979b). Even the sophisticated computer models designed to predict forest productivity, such as DFSIM (Curtis *et al.* 1981), or FORCYTE (Kimmins *et al.* 1983) are based on empirical yield functions derived from correlations between volume, age, and site index.

While such models are useful for management purposes, they typically provide little insight into how various abiotic and biotic site factors interact to regulate forest productivity. For example, a forest manager dealing with a newly planted stand or a fresh clearcut cannot predict productivity unless site index is already known. Even then, site index is a measure of past, not future, productivity and because such relations are developed from past performance of trees on similar sites, they may have little bearing on growth of future managed stands.

One way of describing site productivity would be to use equations combining growth information on the species of concern with information on ecophysiological responses to physical and biological site factors to predict dry matter production. In a sense, this type of model was the objective of much of the ecological modeling conducted by the U.S. International Biological Program. The limited success of such models resulted mainly from their enormous data requirements.

A more pragmatic approach to predicting forest productivity would be to use approaches similar to those used in agriculture. Here, empirical observations of plant growth and direct measurement of physiological responses to various biotic and abiotic factors of the environment are combined in regression estimates of crop yield. Information

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on these responses is then used in combination with climatic and soil data to predict plant growth (e.g. Fixen and Ludwick 1983, Xie and MacKenzie 1986).

The objective of this paper is to further develop a conceptual model of productivity for Douglas-fir forests (Grier *et al*. 1986) showing how water and mineral nutrient availability interact to influence stand productivity.

In this model productivity of Douglas-fir forests is regulated by water and nutrient availability and by interactions between water and nutrient availability. Potential site productivity is largely a function of water availability--maximum site productivity is set by the amount of water available to support transpiring leaf area. The proportion of this potential actually achieved is a function of mineral nutrient availability.

The model is conceptual only and thus has no predictive value. Moreover, the model has no way of accounting for the range of management options available to the forest manager. Thus, the purpose of this model is heuristic; to show how site productivity is regulated by interactions between abiotic and biotic site factors. These interactions usually result in actual productivity being less than the productivity potentially achievable on a given site.

Figure 1. Distribution of Douglas-fir in the North America. Ranges of coastal and Rocky Mt. forms are separarted by a dashed line just north of, and paralleling, the main axis is Vancouver Island.

PRODUCTIVITY OF DOUGLAS-FIR

Douglas-fir is one of the most widely distributed conifers in North America. Figure 1 (from Little 1971) shows that the species ranges over 35° of latitude and from tidewater along the Pacific coast to about 3300 m elevation on the east slopes of the Rocky Mountains, and from about 95°W longitude to 130°W longitude.

Within the range of Douglas-fir, a wide variety of climates, growing seasons and soils are found. For example in Oregon and Washington, Douglas-fir is found on sites with annual precipitation ranging from 3200 mm to 500 mm and January mean temperatures ranging from 5°C to about -4°C (Franklin and Dyrness 1973). Soils supporting Douglas-fir are formed from parent materials ranging from recent alluvium to serpentine (Franklin and Dyrness 1973).

258

Table 1. Observed range of aboveground net primary productivity in Douglas-fir forests.

Region	Low	Average Mg ha^{-1} yr^{-1}	High
Coastal Douglas-fir[†]	1.4	4.2	6.2
Rocky Mountain Douglas-fir[‡]	1.5	3.8	5.3

[†]Calculated from Phase I RFNRP data (Gessel 1982) for stands <100 years old.

[‡]Gower, S.T. and C.C. Grier. Unpublished data on file in Department of Forestry, Univ. Wisconsin, Madison.

Because of the diversity of soils and climates supporting Douglas-fir, productivity of Douglas-fir ecosystems has a wide range as well. Table 1 shows observed primary productivity of some Douglas-fir ecosystems in both coastal and Rocky mountain environments.

Coastal Douglas-fir has a roughly three-fold range of productivity with an observed maximum aboveground net productivity of 21.2 kg ha^{-1} yr^{-1}. The range of productivity of Rocky Mountain Douglas-fir is smaller, with less than a two-fold difference between the observed high and low values. Productivity of Douglas-fir stands on poor sites is about the same in both coastal and Rocky Mountain regions.

NET PRIMARY PRODUCTIVITY

In this paper, forest productivity is defined as net primary production (NPP), a term describing total organic matter production by a forest ecosystem. Net primary production is defined as:

$$NPP = \Delta B + D + G$$

where ΔB is biomass increment, D is litter fall and mortality (or its belowground equivalent), while G is grazing. Net primary production can be divided into above- and below-ground components.

There are two main reasons for using net primary production rather than the more traditional forestry-oriented measures of forest growth such as board foot or cubic volume: (1) carbon allocation to wood and bark is of lower priority than to foliage, fine root, and reproductive tissues. Thus, wood production is not as sensitive to changes in site factors as, for example, production of foliage (Mooney 1972, Waring 1983, Linder and Rook 1984); and (2) foliage and fine roots are the main links between a plant or stand of trees and its external environment. Therefore, the relative amounts of these structures produced by a forest stand provide valuable information regarding the production potential of a stand.

Leaf area appears to be the primary factor regulating ecosystem productivity (Figure 2) and as such, leaf area and factors influencing its amount and efficiency are a primary focus of this paper.

FACTORS REGULATING PRODUCTIVITY OF DOUGLAS-FIR ECOSYSTEMS

Before discussing net primary production and carbon allocation patterns in Douglas-fir ecosystems, it may be useful to discuss the major environmental variables that influence production patterns in Douglas-fir forests. Waring and Franklin (1979) rank temperature, moisture, and nutrients in decreasing importance in their effect on
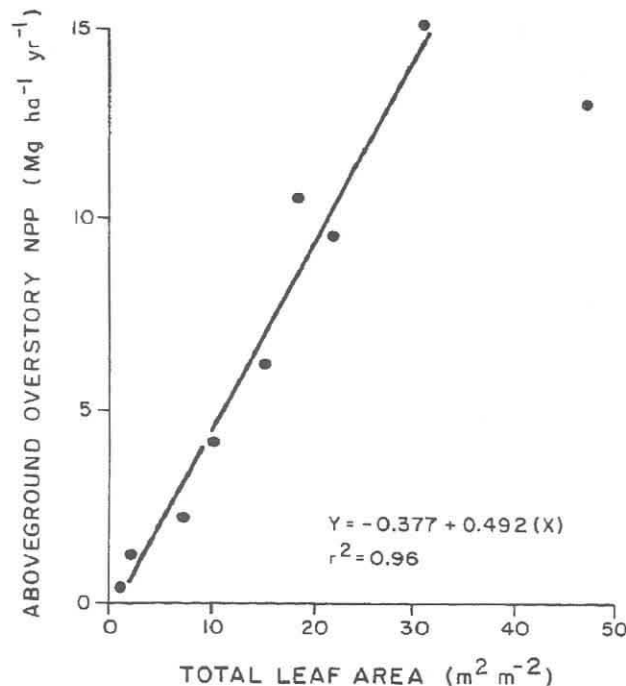
$$Y = -0.377 + 0.492 (X)$$
$$r^2 = 0.96$$

Figure 2. Relation between total leaf area and tree net primary productivity along a transect from the Pacific Coast to the east slopes of the Cascade Mts. in Oregon (from Grier et al. 1986).

the evolution and productivity of Northwest Douglas-fir forests. Presumably, the same factors regulate productivity throughout the range of Douglas-fir. It is difficult to isolate the influence of these factors because of the complex interactions occurring between temperature, moisture, and nutrient availability in the field. However, temperature effects are often indirectly expressed by plant or soil water status and nutrient availability. For example, water uptake by trees is related to temperature, especially in cold soils (Teskey et al. 1984), while nutrient availability is often regulated by temperature effects on decomposer organisms (Alexander 1977).

Water Relations

Most Douglas-fir forests experience water stress to one degree or another during the growing season. Douglas-fir forests occupy two broad climatic regimes characterized by two distinctly different seasonal distributions of precipitation and by temperatures. Forests of the coastal and northern Rocky Mountain Douglas-fir region occupy an environment where relatively little precipitation occurs during the critical summer months (June-September) of the growing season. In Douglas-fir stands in this environment, cessation of cambial cell division coincides with leaf water potentials of about -2.0 MPa (Waring 1969, Lassoie et al. 1985).

Table 2 compares precipitation in the range of Douglas-fir with locations in other geographic regions of the United States. In all other regions including the southwestern range of Douglas-fir, one-third to one-half of the annual precipitation occurs during June, July, and August, the three prime months of the growing season. In the Northwest Douglas-fir region less than 10 percent of the annual precipitation occurs during these three months. Moreover, intense summer rainstorms are rare in this coastal region; thus, much of the summer rainfall does not reach the soil but is intercepted by and evaporates from the canopy. Foliage growth in northwest Douglas-fir stands is generally complete by the end of June, but wood and bark growth may continue through August depending on moisture availability (Lassoie et al. 1985).

The critical implication of this rainfall distribution pattern is that trees in the coastal and northern Rocky Mountain Douglas-fir region must function through the entire growing season on water stored in the soil profile or stem sapwood during winter recharge (Waring and Running 1978). Thus the ability of a soil to retain water for tree growth is a critical factor in determining a site's potential productivity.

Table 2. Amounts and seasonal distribution of precipitation in various regions of the United States.

Region	Location	Total (cm)	% June-August
NE	Montpelier VT	84.6	28.2
SE	Waycross GA	126.0	34.0
NC	Hinckley MIN	73.7	43.0
Sw	Tesuque NM	69.2	54.2
Sw	Santa Fe NM	35.3	45.0
Sw	Flagstaff AZ	60.1	33.5
Sw	Beaver Cr. AZ	63.4	32.4
NW	Detroit OR	129.9	5.7
NW	Medford OR	50.2	7.2
NW	Leavenworth WA	59.0	7.4
NW	Quinault WA	337.1	7.2

Sources: National Climatic Center (1984); Sellers and Hill (1974); Campbell and Ryan (1982).

In contrast to the Northwest, Douglas-fir forests of the southern Rocky Mountains receive a significant proportion of their annual precipitation during the growing season (Table 2). One-third to one-half of annual precipitation in this region occurs during summer thunderstorms. These storms are often intense with substantial runoff but can partially recharge soil water and potentially relieve water stress in trees. Figure 3 shows the effect of summer precipitation on leaf water potential of Douglas-fir on Mt. Taylor, New Mexico. The reduction in water stress in trees in response to the midsummer rains is obvious. The change in leaf water potential is especially dramatic because the summer rains follow the dry, warm, windy weather of May and June with its high evaporative demand (Sellers and Hill 1974).
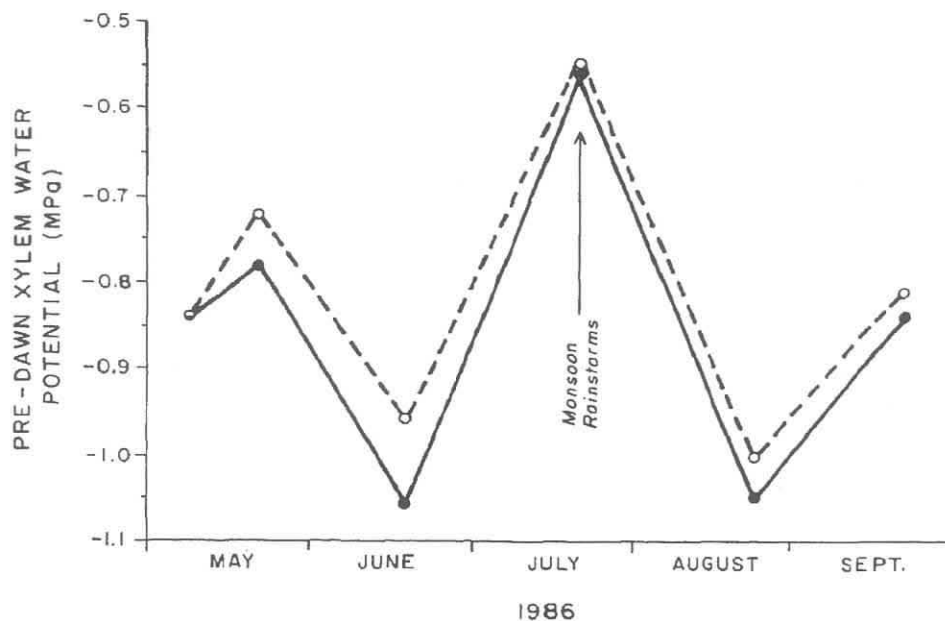
Figure 3. *Changes in pre-dawn leaf-water potential in two plots in an untreated, 60 yr-old Rocky Mt. Douglas-fir ecosystem growing at 3050m elevation on Mt. Taylor, NM. Points plotted are averages of six trees per plot. Foliage was sampled from lower part of upper third of crown. Coefficients of variation ranged between 10 and 20 percent . A large reduction in leaf water stress coincided with the onset of July-August monsoonal rains.*

Nutrition

A large body of evidence shows increased growth by Douglas-fir in response to fertilization, especially nitrogen fertilization (Gessel *et al*. 1969, Miller and Piennar 1973, Atkinson and Morrison 1975, Miller and Harrington 1979, Gessel *et al*. 1979). Increased growth has also occasionally been observed in response to additions of other nutrient elements, particularly phosphorus and sulfur (Gessel *et al*. 1979). Clearly, availability of mineral nutrients plays a role, together with water availability, in regulating productivity of Douglas-fir forests.

Growth response to fertilizer is greater on sites of low native productivity than on more productive sites. Table 3 shows that poorer sites have a greater apparent growth response to nitrogen addition than do more productive sites.

Interactions between moisture and nutrition are an important part of a stand's nutrition regime. Moisture availability can be a major factor limiting site fertility through its effects on decomposition, nutrient mineralization, and ion transport rates (Swift *et al*. 1979, Alexander 1977). For example, Fogel and Cromack (1977) and Edmonds (1979) found decomposition rates to be sensitive to variations in moisture availability in lowland forests of the Pacific Northwest. They reported the lowest decomposition rates occurred during summer. Similarly, Vitousek *et al*. (1982) noted somewhat lower nitrogen mineralization and nitrification rates in Douglas-fir stands during the dry summers of the Northwest, while McColl (1969) reported reduced nutrient availability in Douglas-fir stands

Table 3. Changes in aboveground net primary production in nitrogen fertilization. Production values are averaged for 400 kg urea-N ha^{-1} treatments (from Grier et al. 1986).

Site Class**	NPP (Mg ha^{-1}yr^{-1})			
	Control	Urea-N	AB	% Increase
I	15.2	17.1	1.9	12.4
II	13.9	16.2	2.3	16.2*
III	11.4	14.5	3.1	26.8*
IV	11.8	15.0	3.2	22.8*

*Denotes significant increase at the 95% level.

during the dry summer months. In contrast, increased nutrient availability has been shown to result from summer rains in Douglas-fir dominated forests of the southern Rocky Mountains (Vitousek *et al.* 1982).

Moisture, Nutrition, and Productivity

Figure 4 illustrates a conceptual model of how moisture and mineral nutrition interact to influence site productivity and allocation of assimilated carbon between above- and below-ground components in Douglas-fir forests. In this model, site water balance and nutrient availability regulate net primary production. Temperature also plays an important direct role in regulating productivity. But the impact of temperature is implicitly included in this model through its effects on rates of the various processes described.

The model shown in Figure 4 is driven by the physical environment trees experience during the growing season. The most critical part of the physical environment, is defined in this paper as the balance between available water (growing season precipitation plus soil water storage) and evaporative demand during the growing season.

Leaf surface area is the site where carbon dioxide uptake, water loss, and light interception occur. This critical surface functions as the aboveground interface between a tree and its environment so the greater potential carbon gain associated with a larger photosynthetic surface area should be balanced either by greater water loss via transpiration or by longer periods when stomata are closed or nearly closed. The latter possibility is supported by studies by Brix and Mitchell (1983) showing no difference in leaf or soil water potential between fertilized and unfertilized stands.

Site water balance appears to set an upper limit on the maximum leaf area a site can support. In support of this hypothesis, Grier and Running (1977) observed a strong positive correlation between leaf area of western forest communities and site water balance (Figure 5).
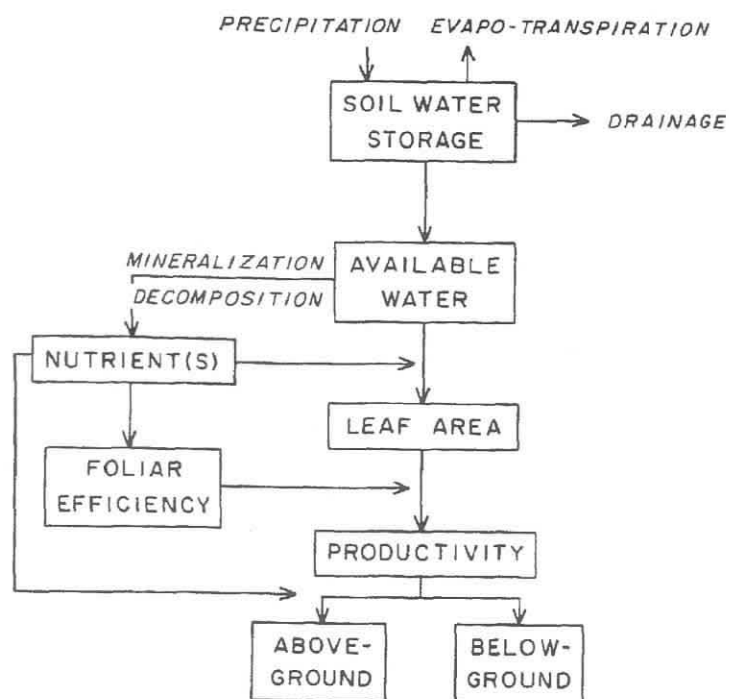
Figure 4. Conceptual model showing how water and nutrient availability interact to regulate productivity of Douglas-fir ecosystems (after Grier et al. 1986).
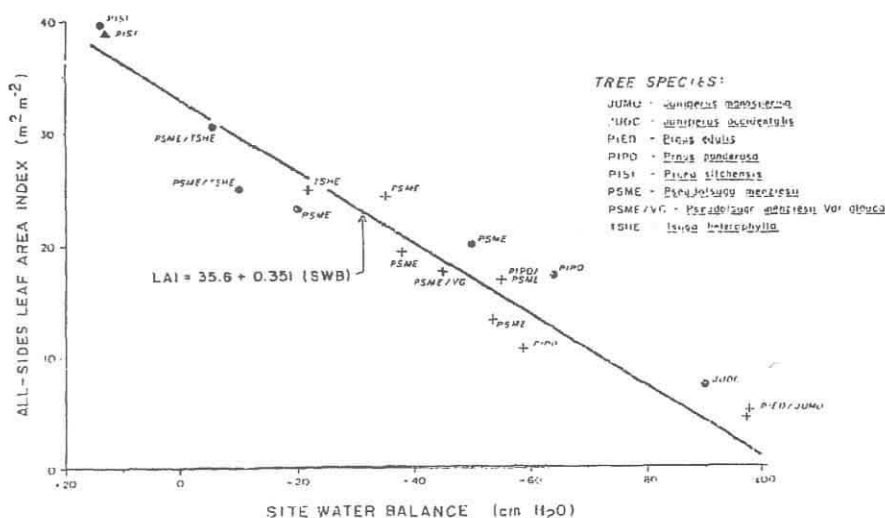

Figure 5. Relation between site water balance and leaf area of various western coniferous ecosystems. Site water balance (SWB) was calculated by subtracting growing season (June - Aug.) evaporative demand (open-pan or evaporimeter evaporation) from the sum of measured available soil water in the rooting zone and growing season precipitation. A negative SWB indicates evaporative demand exceeds available water. Data from Gholz (1982), Grier and Running (1977) and Grier and Gower (unpublished).

Research reported in both the study by Grier and Running (1977) and a subsequent study by Gholz (1982) was conducted in mature stands on sites where foliage color reflected at least adequate levels of mineral nutrients. Because of this, the reported leaf areas were probably near the maximum amount sustainable given the site water balance of the various locations.

More recent work has shown that nitrogen availability can strongly influence the leaf biomass of individual trees and stands (Brix and Mitchell 1983, Grier *et al.* 1984, Figure 6). Specifically, leaf biomass of trees and stands occupying soils having low nitrogen availability has been shown to increase in response to nitrogen fertilization. This increase indicates that nitrogen limitations will prevent a stand from developing the maximum leaf areas potentially sustainable with the site's water balance.
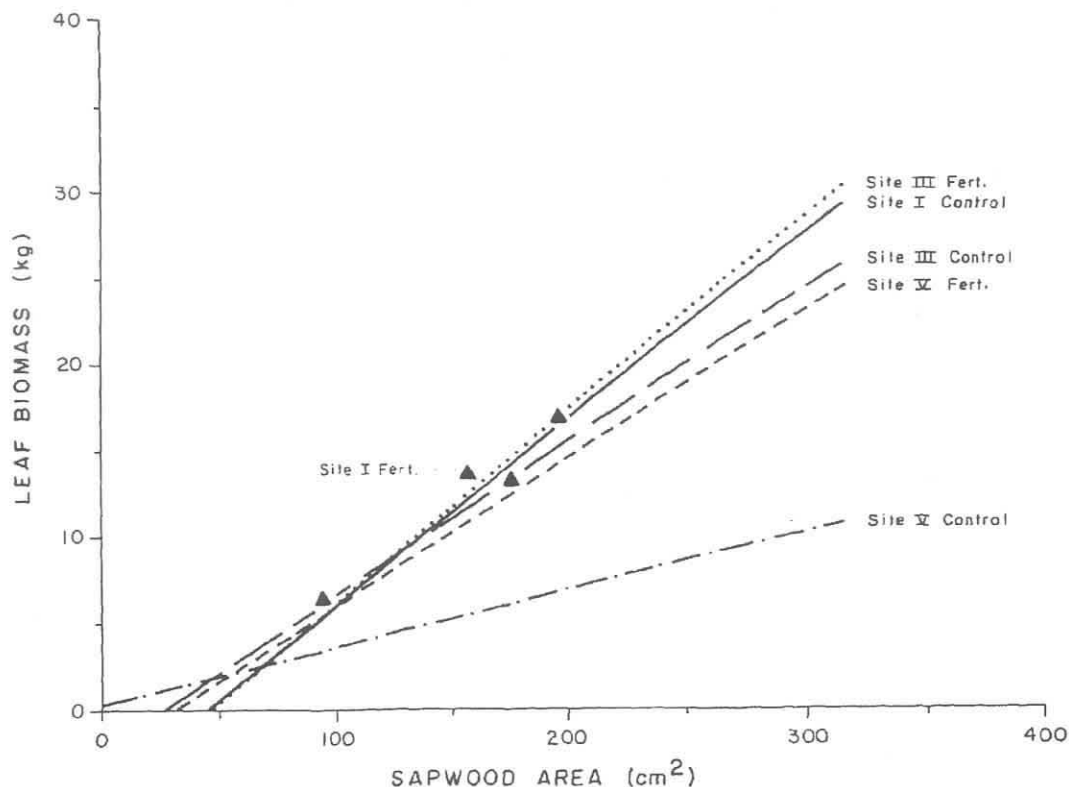

Figure 6. *Regression lines of leaf biomass on a sapwood cross-sectional area for fertilized and unfertilized coastal variety Dougas-fir growing on a range of soil qualities. The increase in leaf biomass in response to fertilization is large on the Site V (King 1966) trees and moderate on the Site III trees. There is no statistically significant difference between regression lines for Site 1 control and Site III fertilized. The four trees plotted from a fertilized Site I appear to cluster around the upper regression lines. Data are for Site V trees from Brix and Mitchell (1983), Site III trees are from Grier et al. (1984), Site I trees are from unpublished data from Grier.*

The response of leaf area to increased nitrogen availability appears to be related to the degree of nitrogen limitation prior to fertilization. A much greater increase in leaf area was observed after fertilizing severely nitrogen-limited stands than was the case for stands on more fertile soils (Figure 6). The greater foliage biomass and area on more fertile or fertilized sites appears to be the result of (1) increased needle size, (2) more needles per shoot, (3) a greater number of current shoots produced (Brix and Ebell 1969, Brix 1981), and (4) greater foliage retention on more fertile sites (Figure 7). Figure 7 shows, in part, the relation between foliage retention and what we term the foliage nitrogen ratio. This ratio is simply the new foliage nitrogen concentration divided by the biomasss-weighted nitrogen concentration of all older foliage. This ratio appears to be an index of the degree of nitrogen redistribution occurring in a tree. As the ratio increases indicating greater reliance on internal redistribution, the foliage retention decreases from 6 years (current foliage plus 5 years older foliage) to 2 years (current
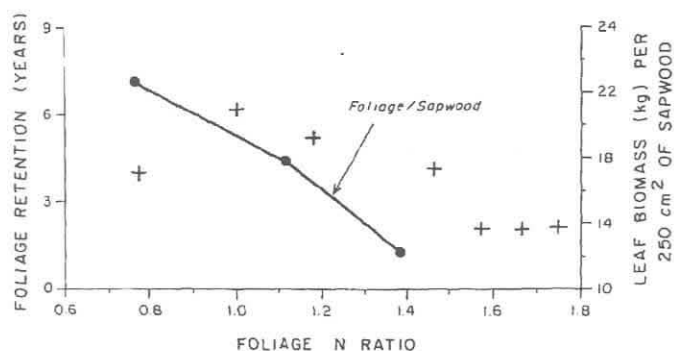
Figure 7. *Relation between foliage nitrogen ratio and foliage retention and foliage mass per unit sapwood for coastal variety Douglas-fir. Foliage nitrogen ratio is the mid-November nitrogen concentration in new foliage divided by the biomass-weighted nitrogen concentration of all older foliage.*

plus 1 year of older foliage). Values given are from coastal variety Douglas-fir. Thus it appears that low nutrient availability (most commonly nitrogen) may prevent a site from supporting the leaf area potentially possible given the site's water balance.

In addition to its effect on leaf area, nutrition appears to influence stand productivity through its effect on photosynthetic efficiency estimated as net primary productivity per unit of leaf biomass (Brix 1983). Brix (1971, 1981) reported significantly greater photosynthetic rates for nitrogen-fertilized Douglas-fir trees growing on poor sites than was observed for unfertilized trees, although the response was short-lived. Similar results have been reported for coniferous species such as *Pinus pinaster* (Keay *et al.* 1968) and *Pinus sylvestris* (Linder and Axelsson 1982). Brix (1981) suggested that the increase in photosynthetic rate in response to nutrient amendment may be explained by one of several mechanisms: (1) increased photochemical reaction as a result of greater chlorophyll concentrations (Brix 1971, Turner and Olson 1976), (2) increased carboxylating enzyme activity (Natr 1975), (3) increased mesophyll conductance of carbon dioxide (Ryle and Hesketh 1969, Brix 1971, Linder and Troeng 1980), or (4) increased carbon dioxide sink demand (Sweet and Wareing 1966).

At any rate, nutrition appears to influence productivity both through its effects on stand leaf area (Figures 6 and 7) and through changes in the photosynthetic efficiency of that leaf area. If nutrients are readily available, then a site's maximum potential leaf area can be achieved. However, as nutrient availability decreases, so does the proportion of the site's potential leaf area actually achieved (Figure 6).

Figure 9 shows the association between aboveground net primary productivity and the foliage nitrogen ratio discussed earlier. Productivity data in this diagram were calculated from Phase I, Regional Forest Nutrition Research Program data on file in the College of Forestry, University of Washington. Nitrogen ratios were obtained by sampling and analysis of foliage from the same stands following the general recommendations of Lavender
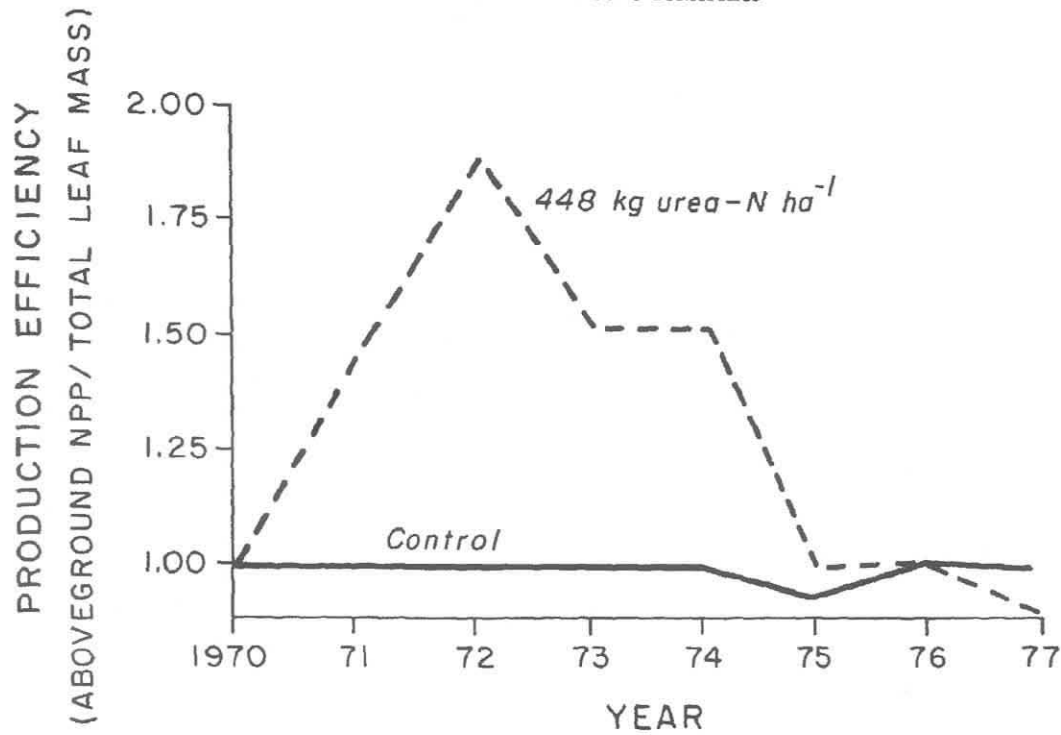
Figure 8. Effects of nitrogen fertilization on the above ground production efficiency of coastal variety Douglas-fir foliage. Production efficiency is kilograms of aboveground dry matter production per kilogram of foliage biomass. Data are from Brix (1983).
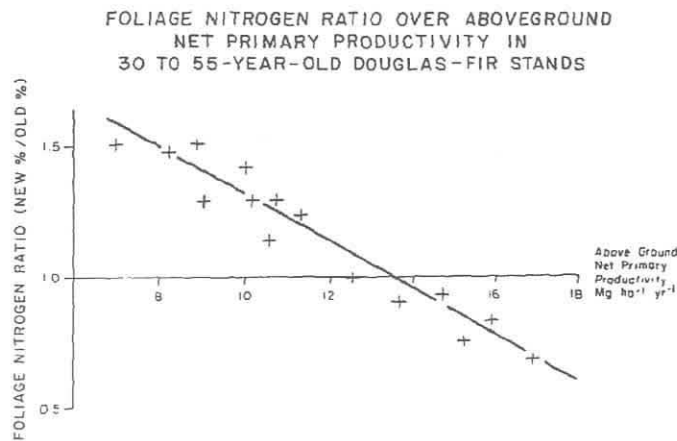

Figure 9. Relation between net primary productivity (NPP) and foliage nitrogen ratio for coastal Dougals-fir ecosystems growing on non-glaciated soils in Oregon and Washington. NPP was calculated primarily from Regional Forest Nutrition Research Program Phase I plot data on file at the College of Forest Resources, Univ. WA. Nitrogen concentrations calculated by sampling and analysis of foliage from the various plots.

267

(1970). Foliage samples were taken in late November from the seventh or eighth whorl down from the top whorl, from the south side of the tree. Net primary productivity was calculated from plot measurement and six-year remeasurement data, using the equation NPP = ΔB/6 + F + M/6 where ΔB was the biomass increment during the six-year interval between measurements, M was mortality in the same interval and F was new foliage production calculated for the final year of the interval. Regressions on stem diameter for woody increment are from Gholz *et al.* (1979); site class regressions of new foliage on stem diameter were adopted from Grier *et al.* (1984). While an association between nitrogen status of foliage and productivity may be inferred, these data do not establish an easy way to detemine site fertility by foliage sampling--the data base is severely limited. The relation does, however, merit further examination.

Nutrition and Carbon Allocation

Apparent productivity of Douglas-fir forests is also influenced by mineral nutrition through its impact on allocation of assimilated carbon to aboveground and belowground portions of the stand. Keyes and Grier (1981) reported aboveground NPP for high and low productivity Douglas-fir stands to be 13.7 and 7.3 $Mg^{-1} ha^{-1} yr^{-1}$, respectively, while belowground NPP on the productive site was 4.1 $Mg^{-1} ha^{-1} yr^{-1}$ versus 8.1 $Mg^{-1} ha^{-1} yr^{-1}$ on the poorer site. In similar stands Vogt *et al.* (1985) observed a greater allocation of carbon to belowground components in control than urea-nitrogen fertilized stands of Douglas-fir (Figure 10).

In the study by Vogt *et al.* (1985) average fine root biomass of the repeatedly fertilized stand was about 25 percent of that of the control stand. Seasonal fluctuation in fine root biomass was also much reduced. An estimate of fine root production may be obtained by summing statistically significant increases or decreases in fine root biomass over a season. Here, estimated fine root production by the control stand was about 8 Mg $ha^{-1} yr^{-1}$ compared with about 4 Mg $ha^{-1} yr^{-1}$ for the fertilized stand. This 4 Mg $ha^{-1} yr^{-1}$ decrease in belowground production accounted for about 70 percent of the 5.6 Mg $ha^{-1} yr^{-1}$ aboveground growth response.
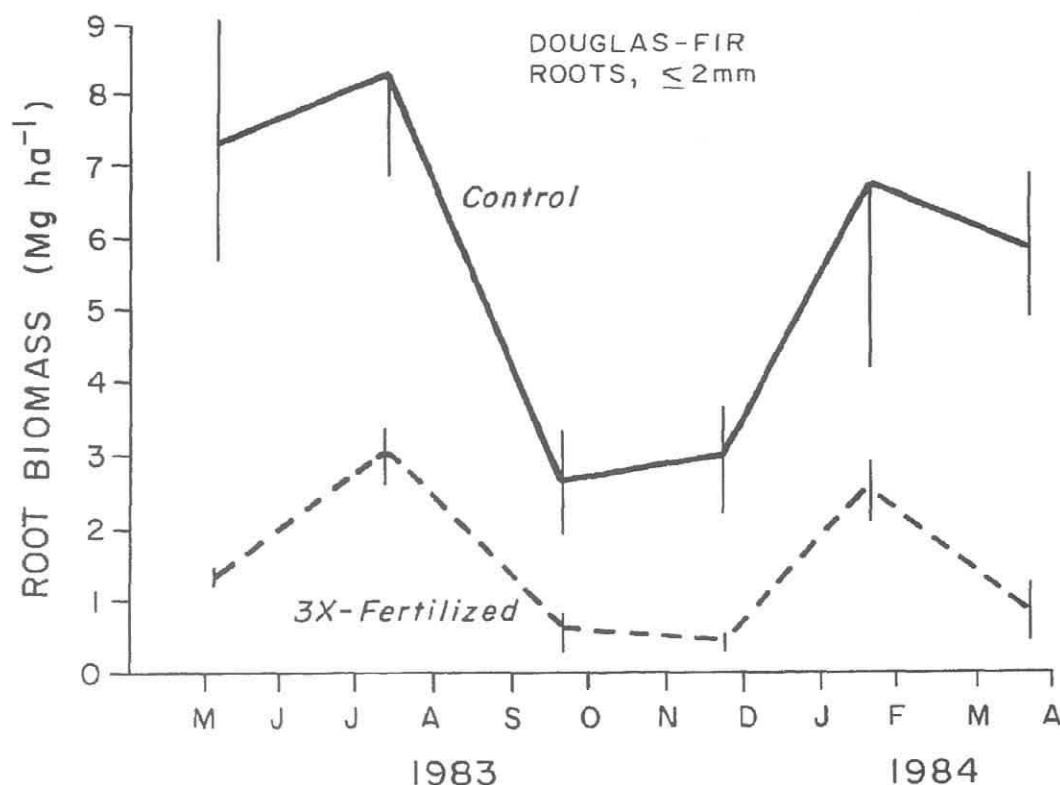

Figure 10. Effects of repeated nitrogen fertilization on the fine root biomass of a Site IV coastal variety Douglas-fir ecosystem in western Washington. Three applications of urea (46-0-0) were made at 3-yr intervals. Applications were 448,224 and 224 kg ha^{-1} respectively (from Vogt et al. 1985).

Table 4. Changes[†] in mycorrhizal root tip biomass in soil of Site IV Douglas-fir stand following fertilization[‡] with total of 0.45 kg ha^{-1} urea-N. Data from Friedman-Thomas (1986).

| Soil Horizon | Root Tip Biomass, 10 June 83, Mg ha^{-1} | | | |
| | Control | | Fertilized | |
	$\bar{x}$	$S\bar{x}$	$\bar{x}$	$-S\bar{x}$
O$_2$	0.49	0.14	0.35	0.11
A$_1$	0.66	0.14	0.49	0.14
B$_I$-B$_3$	0.38	0.09	0.33	0.11
Total	1.53	0.37	1.17	0.36

[†]Fertilized and control plots were not significantly different when sampled 15 March 83. Comparable March values were 900 kg ha^{-1}.

[‡]Fertilization: 20 March 83, 0.22 Mg ha^{-1} urea-N; 13 April 83, 0.23 Mg ha^{-1}.

In an experiment designed to show effects of increased fertility on fine roots and mycorrhizae, Friedman-Thomas (1986) determined fine root and mycorrhizal biomass in six plots in a 60-year-old Site IV (King 1966) Douglas-fir stand near Matlock WA on 16 March 1983. Three of the six plots were then randomly chosen for two equal applications of urea totaling 0.45 Mg ha^{-1}. Applications were made on 20 March and 18 April 1983. Fine root biomass in the six plots was again determined on 10 June 1983. Results given in Table 4 show that mycorrhizal root tip production in the fertilized plots was roughly 75 percent of that in the unfertilized plots. Again, the reduction in belowground growth corresponded with increased aboveground productivity so possible toxic effects of fertilization on root systems do not appear to be important. An important point here is the rapid response in carbon allocation to changes in available nutrients.

CONCEPTUAL MODEL

Our conceptual model of Douglas-fir productivity is given in Figure 4. As previously noted, the model is simple in concept. We are proposing this model as a series of linked hypotheses we feel are experimentally testable. Hypotheses subject to systematic experimental analysis are:

1) Potential productivity of Douglas-fir ecosystems is fixed by their physical environment; specifically, the growing season balance between evaporative demand and water available to support transpiration regulates leaf area which regulates productivity.

2) The proportion of this physically determined potential actually achieved is a function of mineral nutrient availability. This is a function of both site water balance and soil chemical properties. On infertile sites trees cannot obtain sufficient nitrogen to develop potential leaf area.

3) Mineral nutrition also regulates the photosynthetic efficiency of the leaf area the site can support. The greater the site fertility the greater the photosynthetic efficiency.

4) Apparent site productivity of Douglas-fir is also a function of nutrient availability. On infertile sites, a greater proportion of assimilated carbon is allocated to roots than on more fertile sites.

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